

## Some recent investigations on the evaporation of water from plants.<sup>1</sup>

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At the meeting of the American Association for the Advancement of Science in August, 1891, a paper was read by Prof. Bessey and myself on "Transpiration; or, the loss of water from plants." In that paper we gave in a very condensed way the condition of this problem at that time.

We called particular attention to two papers by Dr. Alfred Burgerstein, published in 1887 and 1889, and called "Materials for a monograph relating to the phenomena of transpiration of plants."<sup>2</sup> Dr. Burgerstein's papers make a most valuable contribution to the literature of transpiration, and are invaluable to one who desires to make a critical study of the subject.

A pamphlet by Dr. Oscar Eberdt<sup>3</sup> is also a masterly presentation of the subject, and contains the record of many valuable experiments.

The investigations recently carried on by M. Henri Jumelle and published in the *Revue générale de Botanique*, have afforded us a clearer insight into the relation existing between evaporation and assimilation. M. Jumelle shows<sup>4</sup> that a ray of light, passing through the chlorophyll of a leaf, is partly used in assimilation and partly in chlorovaporization. If the supply of carbon dioxide is taken away from the plant, assimilation is, of course, stopped, and more of the energy of the absorbed light ray is left free to affect chlorovaporization.

In a series of experiments which I conducted on the internal temperature of plants, I found that a ray of light, after passing two parallel panes of clear glass three-fourths of an inch apart, filled between with a saturated solution of alum in distilled water, had a remarkable calorific effect on plant tissue rich in chlorophyll, quickly raising the internal temperature from 3° to 5°C. higher than the air. Direct light (that is

<sup>1</sup>Read before the Botanical Seminar of the University of Nebraska, April 15, 1893.

<sup>2</sup>Materialien zu einer Monographie betreffend die Erscheinungen der Transpiration der Pflanzen. Verh. K. K. Zool.-Bot. Gesells. Wien.

<sup>3</sup>Die Transpiration der Pflanzen und ihre Abhängigkeit von äusseren Bedingungen. Marburg 1889.

<sup>4</sup>l. c. 1889, no. 1.

light not passed through glass or alum solution) had a much greater effect. In some cases, as in the petiole of the banana leaf in direct sunlight, the temperature was  $20^{\circ}\text{C}$ . higher than the air. The temperature decreases as the intensity of the light.

Green tissue warms much more rapidly than it cools. Living green tissue of cactus and castor-oil plant warms more rapidly than dead tissue of the same, but cools at about the same rate. The dead tissue follows very closely the temperature fluctuations of an equal bulk of water enclosed in a smoked glass cylinder. Checking evaporation causes a rise of temperature proportional to the decrease of evaporation.

The investigations that I made last year on the evolution of bubbles of gas by green plants, in water, exposed to light,<sup>5</sup> showed conclusively that this evolution of bubbles, from such plants as *Myriophyllum*, was not the result of assimilation, but the calorific effect of the absorbed light ray.

These few facts, taken from my reports presented to the Seminar last year, are certainly, as far as they go, confirmatory of M. Jumelle's results.

M. Jumelle's next work was on the influence of anæsthetics on the transpiration of plants. His apparatus was simple, consisting of a bell glass set in a dish of mercury. The openings through the top of the bell glass for the introduction of anæsthetic and carbon dioxide were under absolute control. The plant experimented with was placed under the bell glass and the water evaporated collected by calcium chloride. In the experiments on chlorophyllian transpiration in the presence and absence of carbon dioxide, the loss of weight of the plant was noted, as well as the gain in weight of the calcium chloride. But in the experiments with anæsthetics he considered that the loss of weight of the plant would not exactly represent the amount of water evaporated because of the weight of the ether absorbed by the anæsthetized leaves. In all cases M. Jumelle first determined the amount of anæsthetic necessary to stop assimilation without killing the plant. At the close of the experiment the plant was washed in water, after which, if the experiment had been successful, assimilation started again. The results of these investigations showed that in the light the effect of the anæsthetic was

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<sup>5</sup>Extract published in Publication II of the Nebraska Academy of Sciences, 1892.

to increase transpiration. This Jumelle considered to be due to the fact that the anæsthetic, by affecting the chloroplast, stopped assimilation; thus more of the energy of the absorbed light ray was used in chlorovaporization. In the dark M. Jumelle found that the anæsthetized plant lost less water than the normal plant, but failed to come to any definite decision as to why this should be so.

MM. Verschaffelt<sup>6</sup> criticised M. Jumelle's methods of experimenting, and questioned his conclusions in regard to the relation of carbon dioxide to evaporation in the light and in the dark. They used in their investigations a modification of the Kohl transpiration apparatus. The modification consisted simply of a glass vessel containing culture fluid or water into which the roots, or in some cases the cut end, of the plant extended. The evaporation was measured by the loss of weight of the apparatus; of course no water could escape except through the plant. In the case of assimilating plants the water evaporated was collected by calcium chloride. This was because the Verschaffelt brothers considered that the increase in weight of the plant due to assimilation must be taken into account. They concluded that the transpiration of a plant in an atmosphere free from carbon dioxide is greater than in air containing it, both in the light and in the dark. Further, that the presence of carbon dioxide in the air decreases evaporation in the light independently of assimilation.

M. Jumelle made a critical discussion of the MM. Verschaffelt brothers' investigations and conclusions.<sup>7</sup> He went over his experiments with apparatus meeting all their objections and not only proved the correctness of his own former results but also showed where the MM. Verschaffelt made their mistake.

This article is followed by a final one<sup>8</sup> giving the results of further investigation of the points in controversy which results fully confirmed Jumelle's former conclusions, namely, that, in the light, the presence of carbonic acid gas in the air around the plant devoid of chlorophyll has no effect on transpiration. The influence of carbonic acid gas is exerted exclusively upon chlorophyllian transpiration.

The absence of carbonic acid gas from air supplied to green

<sup>6</sup>Bot. Centralb. XLII (1890). 373-374.

<sup>7</sup>Revue gén. de Bot. 1891. nos. 30 and 31.

<sup>8</sup>Revue gén. de Bot. Juillet 1891.

plants in light causes an increase in transpiration. This may be explained by the fact that the energy of the light rays absorbed by the chlorophyll, which energy is ordinarily partly used in assimilation, is here wholly free to effect transpiration.

In the BOTANICAL GAZETTE for February, 1893, is an article by Albert Schneider on the "Influence of anæsthetics on plant transpiration." In this article Mr. Schneider attempts to show how M. Jumelle came to erroneous conclusions. Quoting from Mr. Schneider's article: "Jumelle has lately been carrying on a controversy with Verschaffelt who maintains that ether increases transpiration in the dark as well as in the light. This Jumelle has attempted to disprove in his final paper on anæsthetized plants."

Mr. Schneider has evidently been a little careless in his reading or else has failed to indicate where he received his information. The only controversy, so far as I know, between M. Jumelle and MM. Verschaffelt has been on the relation of carbon dioxide to transpiration in the light and in the dark as before mentioned in this paper. M. Jumelle's final article (l. c.) has nothing in particular to say in regard to anæsthetized plants but deals wholly with the problem under discussion between himself and MM. Verschaffelt. Further Mr. Schneider says: "By way of criticism it must be pointed out that, in the first place, Jumelle as well as Verschaffelt used only portions of plants in their experiments and hence their conclusions are of little practical value." This criticism might be justly made had these investigators used, for the measure of evaporation, as did Mr. Schneider, the amount of water absorbed by the roots. When the loss of water is measured as they measured it, the results obtained from branches, properly prepared and supplied with water, are just as trustworthy as the results obtained from whole plants. M. Jumelle in his first reply to MM. Verschaffelt says distinctly that he used *entire* plants in order to exactly meet the conditions of the experiments performed by MM. Verschaffelt. Later however both investigators used branches as well as whole plants.

Turning now to Part III of Mr. Schneider's article, "Experiments on transpiration of entire plants"; first of all he has made a very great mistake in assuming that the amount of water absorbed by the roots of a plant represents the amount "transpired." By consulting Dr. Oscar Eberdt's inves-

tigations in the article mentioned in the first page of this paper it will be seen that this relation, even under the most favorable conditions is far too general and fluctuating to be of any value whatever as an exact measure of evaporation. This difficulty alone is sufficient to make Mr. Schneider's results practically valueless as far as transpiration is concerned.

Further, M. Jumelle took special pains to ascertain the amount of anæsthetic that was required to stop assimilation *without killing the plant*, and always tested the plant after the experiment in order to be certain that it had not been killed. Mr. Schneider took no such precaution in his experiments, but says that he took "no special notice of the amount of anæsthetic used;" and further says that after a time the plants exposed were killed. He is thus dealing with plants under entirely different conditions from those maintained by M. Jumelle; hence, even had Mr. Schneider's measure of transpiration been reliable, his results could have no direct bearing on M. Jumelle's results or conclusions.

In part IV, "Experiments on transpiration of leaflets," Mr. Schneider estimates the transpiration by weighing the leaflets and noting the loss. The slight objection to this I have before mentioned and will let it pass. The second objection is that the leaflets were not supplied with water and the amount of anæsthetic supplied was too great to meet the conditions of Jumelle's experiments. The fact that the leaves were not supplied with water is alone sufficient to make the results at least extremely doubtful. It is unnecessary to discuss Mr. Schneider's article further at this time. It is certainly quite evident that his results do not affect M. Jumelle's conclusions.

Coming back now to the condition of the problem of "transpiration" as left by M. Jumelle. First, the presence or absence of the usual amount of carbon dioxide in the air has no effect on the transpiration of chlorophyll-less plants either in light or dark. Here certainly "transpiration" has no relation to assimilation. We know further that etiolated plants lose water much more rapidly in strong light than in the dark.

Plant.	Darkness.	Diffused light.	Sunlight.
<sup>10</sup> Zea Mais (etiolated) . . . . .	106	112	290 <sup>mm</sup>
Zea Mais (green) . . . . .	97	114	785 <sup>mm</sup>

<sup>9</sup>See also Dr. Alfred Burgerstein's remarks on this subject page 67, part 2 of article referred to on first page of this paper. Also paragraph 748 on page 279 of Goodale's Phys. Bot.—Also Vines' Phys. Bot. page 99.

<sup>10</sup>Experiments by Wiesner, page 110, Vines' Phys. Bot.

Here again it is evident that "transpiration" is independent of assimilation. The greater loss from the green maize plant in light as compared with the etiolated one Wiesner refers to the fact that the rays of light absorbed by the chlorophyll of the green plant are converted into heat, a conversion which is not effected to the same extent by the etiolated plant. If we now stop assimilation by any means the  $785^{\text{mgr}}$  lost in the sunlight from the green *Zea mais* would, according to M. Jumelle, be increased, showing again that transpiration does not increase directly with assimilative activity in the protoplasm, but, on the other hand, decreases as assimilative activity increases. It is also known that as the vitality of the protoplasm decreases it loses its power of retaining water. We are justified, then, in maintaining that the excess of the loss of water in the light over the loss in the dark, both in green and etiolated plants, is due to the calorific effect of the light and is therefore purely a physical process, *evaporation*.

Now in regard to the relation of anæsthetics to "transpiration" in the dark. M. Jumelle's results show that the anæsthetized plant loses less water in the dark than the normal plant. This fact M. Jumelle says he can not satisfactorily explain. These results so far as I know have not been questioned but rather confirmed by other observers. I think, however, that all have made errors in conclusion on this point which I shall endeavor to correct. The influence of an anæsthetic on protoplasm in the dark is more marked than the influence of the same dose in the light. One would conclude from the data at hand that anæsthetized protoplasm has less power than normal protoplasm of resisting evaporation. We would expect the anæsthetized plant to lose more water in the dark than the normal plant.

In an investigation that I made, recently, on the relation of sulphuric ether to the opening and closing of stomata, I found that, even in moderately strong diffused light, a strong dose of ether nearly closed the stomata. In weak diffused light the action was very marked, especially so in the leaf of *Canna Indica* in which the stomata closed almost instantly when brought under the influence of ether. These experiments were repeated many times with essentially the same results. If, as these experiments indicate, the stomata of anæsthetized plants remain closed in the dark, we could readily understand why

the water-loss should be less. In order to avoid this difficulty (and another possible one, viz., the taking of water from the outer exposed cells of a plant in air containing ether, by the inner less exposed ones), I used moss plants (*Mnium* sp.) set in small metal pots. The leaves were large and composed of a single layer of thin walled cells. I first determined the maximum dose of ether that might be administered to a plant without causing death. The plants were put under the influence of ether, then removed to ordinary air, and the evaporation compared with that of normal plants. In strong diffused light and sunlight the leaves of the anæsthetized plant dried and curled rapidly while the normal plant was much more slowly and less affected. In weak diffused light the anæsthetized plants lost water most rapidly as shown by the drying and curling of the leaves while the normal plants were only slightly affected. In the dark the same results were obtained as in weak diffused light. The drying of the plant is most rapid if it is first put under the influence of ether, then removed to dry air containing only a small amount of ether. After the experiments the anæsthetized plants were washed in water and fully regained their former freshness, showing that the investigations had been made on living subjects.

The results of my experiments indicate that the effect of ether on the exposed plant cell, in the dark as well as in the light, is to decrease its power of retaining water and thus increase the supply for evaporation. In the dark as well as in the light evaporation increases as the activity or vitality of the protoplasm decreases. We have good reason to believe that "transpiration" would be nothing in a perfectly saturated atmosphere if it were possible to obtain such, and that it is nothing in all wholly aquatic plants. It is evident, therefore, that so-called "transpiration" is not something which protoplasm *does* but something which it *resists*. It is not a physiological function or activity of protoplasm although it may have a physiological relation to the normal development of certain plants or parts of plants. Transpiration is nothing more than *evaporation*.

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